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The Relation of Temperature to Growth and Respiration in the Potato Plant

John Bushnell
Division of Horticulture

UNIVERSITY FARM, ST. PAUL

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THE RELATION OF TEMPERATURE TO GROWTH AND RESPIRATION IN THE POTATO PLANT

By JOHN BUSHNELL[1]

I. INTRODUCTORY LITERATURE REVIEW: RELATION OF TEMPERATURE TO TUBER YIELDS

There is convincing evidence that temperature is frequently a limiting factor in yields of the potato *(Solanum tuberosum)*. From an ecological viewpoint, Orton (18) summarized the facts showing that this crop thrives best at relatively cool temperatures. He pointed out: (1) in the Andean region, probably the native habitat of the potato, the mean temperature of the warmest month is only 61° F.; (2) within the United States the highest yields are secured in the regions with the coolest summer temperatures; and (3) of the regions where the crop has been introduced, it perhaps yields best in Scotland and northern Europe, where the mean July temperatures are about 60° F.

Smith (21) analyzed the relation of weather to yields of potatoes in the United States in much greater detail. He showed by maps and isotherms a striking relation between mean July temperatures and average acre yields. Figure 1, which is similar to one of the maps of Smith, shows the ten-year average yields for each state and the isotherms of highest normal temperatures during the growing season. The relation between yield and temperature is obvious. The variations in yield along any given isotherm are largely due to variations in production practices. The yields in the southern states are generally lower than in the northern states traversed by the same isotherms. This is due to the practice of growing the potato in the south as a spring or fall crop, thus avoiding the period of highest temperatures but also shortening the growing period so that the crop is harvested immature and the yields are correspondingly lowered. In this region the isotherms of Figure 1 are shown as broken lines. Along the Atlantic coast the yields are generally higher than in the interior states. A large part of this may be attributed to the influence of the ocean on the temperature as indicated by the trend of the isotherms, but in part this higher yield is due to economic factors. Even without correcting for these variations, there is a conspicuous relation between temperature and yields per acre. This is roughly summarized in Table I.

[1] Formerly of Division of Horticulture.

TABLE I

APPROXIMATE RELATION OF HIGHEST NORMAL TEMPERATURE TO POTATO YIELDS AS INDICATED BY FIGURE 1

Highest normal temperature	Average yields per acre
Deg. F.	Bu.
Below 65	200
65-69	170-100
69-73	120- 80
Above 73	80- 60

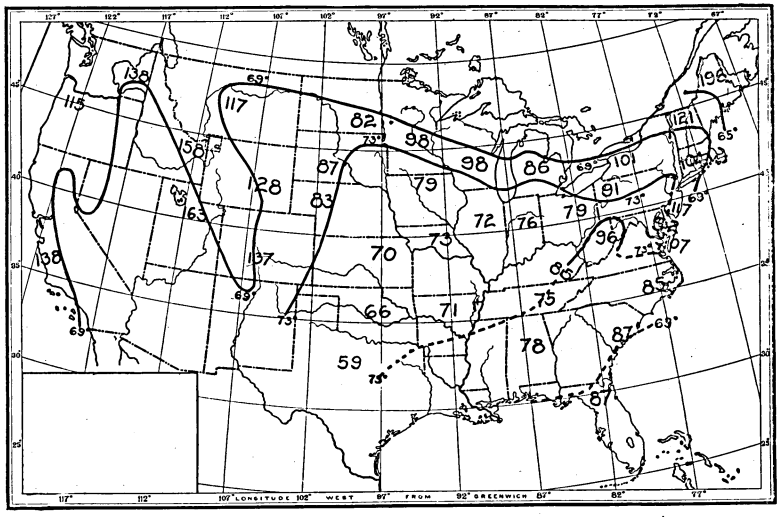

Fig. 1. Average Yields of Potatoes and Isotherms of Highest Normal Temperature During the Growing Period of the Crop (From Data of Smith (21), Bigelow (2), and U. S. Dept. of Agr. Yearbook (25)

Seasonal variations in temperature also have an important bearing on potato yields. Smith (21) attempted to define quantitatively the effect of the different factors of climate by applying statistical treament to records of temperature and rainfall and potato yields in Ohio. He found that temperature gave a more significant correlation with yield than did rainfall, high temperatures being associated with low yields. Furthermore, July temperatures were more important than any others. This led to his suggestion that the crop has a critical period in July when the plant is particularly sensitive to high temperature. The concept of a critical period has not yet been confirmed by other investigations, and it should be pointed out that it is possible to explain the results by another equally plausible hypothesis. The critical period occurred in July, the period of highest temperature in Ohio (see Bigelow, 2). The correlation method used by Smith merely showed that the yield of potatoes was more affected by *departures* from average temperature in July than by corresponding departures in other months.

Thus departures above the normal in July were high enough to be seriously detrimental, while equal departures at other times did not bring the temperature to such a high point and therefore were not so serious. Smith's correlations show that high temperatures depress potato yields, but they do not prove that this is related to a critical period in the growth cycle.

Observations on potato plants grown under greenhouse conditions confirm the climatological evidence that the species is sensitive to differences in temperature. Hardenburg (9) grew crops in two greenhouses, one operating at an average temperature of 15.3° C., the other at 20.3° C. The soil moisture was maintained uniform and equal in the two houses. Larger yields of tubers were produced at the lower temperature.

Fitch (8) grew plants at soil temperatures of 50°, 65°, and 80° F. He published no measurements, but his photographs show the plants growing at 65° to be most vigorous. At the Wisconsin experiment station a larger number of soil temperatures have been available and a more extended series of observations reported. The experiments at Wisconsin have been conducted from the pathologist's viewpoint, but considerable data have been published on uninfected plants. Richards (19) gave measurements on young plants and stated that in a series grown nearly to maturity, soil temperatures of 15° to 18° C. were most favorable. Jones, McKinney, and Fellows (10) gave data in more detail on plants grown to maturity. Table II is from their figures. An interesting feature of these data is the difference in the optimum temperature of the top and the tubers. The largest yield and the largest number of tubers were produced in a soil temperature of 18° C. while the largest weight of green tops was found at 21° C.

TABLE II

INFLUENCE OF SOIL TEMPERATURE ON THE POTATO PLANT. DATA OF JONES ET AL. (10).

Soil temperature, C.	11-12	14.5-15	18	21-21.5	24-25	27-28.5	27-30.5
Av. number of tubers per hill.....	8.2	12.5	11.2	12.5	12.8	14.4	10.2
Av. weight of tubers per hill, gr...	22.0	42.7	56.0	54.2	51.0	25.0	9.5
Av. weight of tubers, gr.	2.6	5.4	7.0	6.0	4.2	2.1	.8
Av. weight of green tops per hill, gr.	55.1	77.0	82.2	89.0	87.0	70.0	50.0
Av. number of stems per hill.....	2.8	3.6	4.2	4.6	4.0	3.2	2.8
Av. height of stems, cm.	22.0	23.0	22.6	23.5	25.0	30.2	14.0
Av. diameter of stems,* cm.	.71	.85	.79	.77	.67	.39	.33
Av. days for plants to come up...	23.0	17.5	12.8	12.8	12.8	16.5	24.6

* Dr. Jones wrote in a letter, September 18, 1925, that the measurements in this line were incorrectly reported and suggested the correction used here.

In summarizing these observations from widely different viewpoints and widely different methods of approach upon different varieties,

there is a rather remarkable agreement on the effects of temperature on this crop. Thus, in regard to the optimum for yield:

Orton's compilation suggests about 16° C.
Smith's surveys indicate 18° or lower
Hardenburg's data give nearer 15° than 20°
Fitch's data suggest about 18°
Jones, McKinney, and Fellows found 18°.

These all point to an optimum for tuber production between 16° and 18° C. Furthermore, these diverse sources agree that yields decline rapidly with increase in temperature above the optimum.

Rôle of moisture.—It is not a simple matter to separate accurately the effect of temperature from that of moisture in studies of the type reviewed here. The writer has found no climatological evidence that moisture, of itself, is an important factor except in arid regions. Potatoes are a commercial crop in the arid west as well as in regions of high rainfall and high humidity. Smith (21) found no really significant correlation of rainfall with yield of potatoes in Ohio. Furthermore, the detrimental effect of high temperature was not definitely associated with rainfall; high temperature depressed yields whether the rainfall was above or below normal. His correlations showed that in Ohio temperature was a more important factor than precipitation.

Humidity has less bearing on the potato crop than rainfall. Excellent yields are obtained under arid conditions, and at the other extreme, excellent yields are produced in humid, maritime climates, particularly in Europe. However, direct experimental evidence bearing on relative humidity, especially at high temperatures, has not been found in the literature. Consequently, a preliminary study bearing on this point was carried out before proceeding with studies on temperature. Potato plants were grown during the summer of 1922 in the chambers later used for the temperature experiments. Three of these chambers were set to operate at 30° C. with relative humidities of 58, 74, and 100 per cent. The results agreed with expectation. In all three chambers the plants produced small leaves and no tubers—typical high temperature responses. No significant differences were observed that could be attributed to differences in humidity.

It is thus evident that temperature of itself, independent of moisture, is an important factor in the yield of potatoes. The following experiments were undertaken, therefore, as a study of the effects of temperature on the plant as a whole, but with particular reference to the physiological mechanisms associated with tuber growth. More specifically, the aim was to find the physiological basis for the decrease in tuber yields at temperatures above the optimum.

II. GROWTH RESPONSE AT CONTROLLED TEMPERATURES

EXPERIMENTAL METHODS

The experiments were carried out in specially constructed, thermoregulated chambers in a greenhouse. Preliminary experiments were run during 1922. The two main plantings were grown in the spring of 1923. The spring months are particularly favorable for greenhouse work, supplying both excellent light and temperatures low enough for studies on a species with a low optimum temperature. The first experimental set of 1923, called series A, was planted in March, series B early in April, and both were discontinued the last week in May.

In order to have a large number of individuals, the plants were grown in eight-inch pots. These appeared to be entirely satisfactory. Tubers of the Early Ohio variety were cut and planted directly in the pots in ordinary sandy soil. The difficulties encountered in securing uniform plants were pointed out in an earlier note (Bushnell, 6). The plants were kept under the same conditions until they were all above

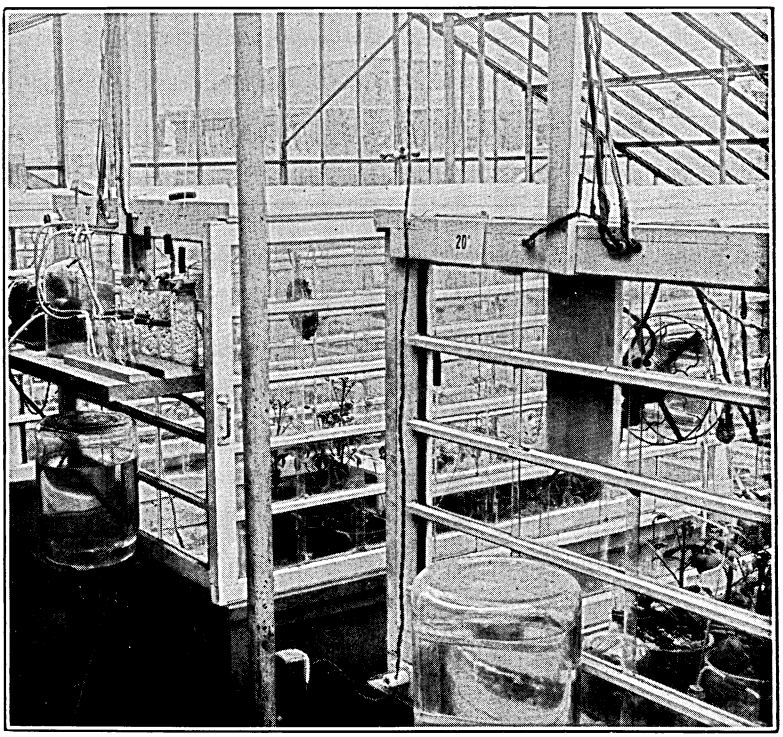

Fig. 2. Theormoregulated Chambers Showing General Features of Construction

ground. Then they were sorted into four equal groups and moved to four chambers operating at 20°, 23°, 26°, and 29° C. In the experimental chambers the plants were watered and measured daily.

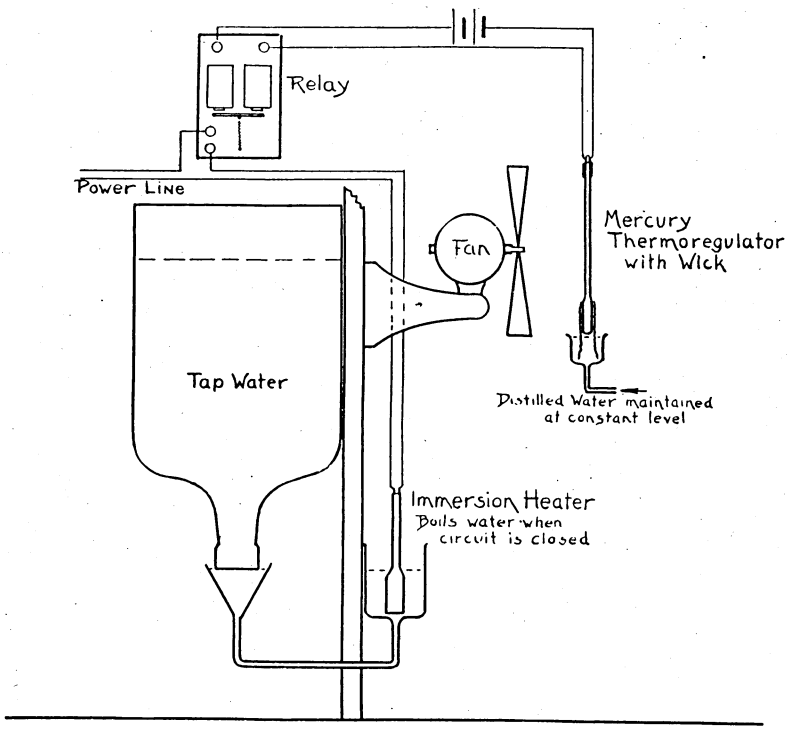

Fig. 3. Diagram of Humidity Regulator

The four chambers were constructed of hotbed sash set on a base 16 inches high. The general features of their construction can be seen from Figure 2. The temperatures were controlled by mercury thermoregulators (Harvey type) operating electric heaters through relays. The heaters were units designed for an electric stove, and being of the resistance wire type did not give any large amount of light. The air was stirred by an electric fan. The humidity control is diagramatically shown in Figure 3. Mercury thermoregulators were adapted to humidity control by covering the bulb with wet linen cloth and placing it in the draft from the fan. By this arrangement they were analogous to wet bulb thermometers. Each was set 5° C. below the air temperature of the chamber, thus maintaining the relative humidity at about 60 per cent in each. As a preliminary experiment had indicated that differences in humidity were not important, this degree of humidity was arbitrarily selected because it was easy to maintain and approximated outdoor humidities.

The temperature range of 20° to 29° was as wide as could be used under the conditions at hand. Refrigeration was not available, so the lowest temperature was determined by the temperature of the greenhouse, and 29° C. was the highest point at which the humidity could be maintained at 60 per cent without excessive condensation of moisture on the glass walls.

The usual difficulties were encountered in controlling the temperature and humidity in chambers of this size. These difficulties have been considered in detail by Tottingham (23). In bright sunlight there was a tendency for the temperature to rise. During April this was satisfactorily controlled by covering the surface of the soil and all dark objects in the chambers with white paper, but during May it was necessary to whitewash an area of the greenhouse roof, partially to shade the chambers during the middle of the day. There was occasional difficulty from the thermostats, chiefly at the relays, due

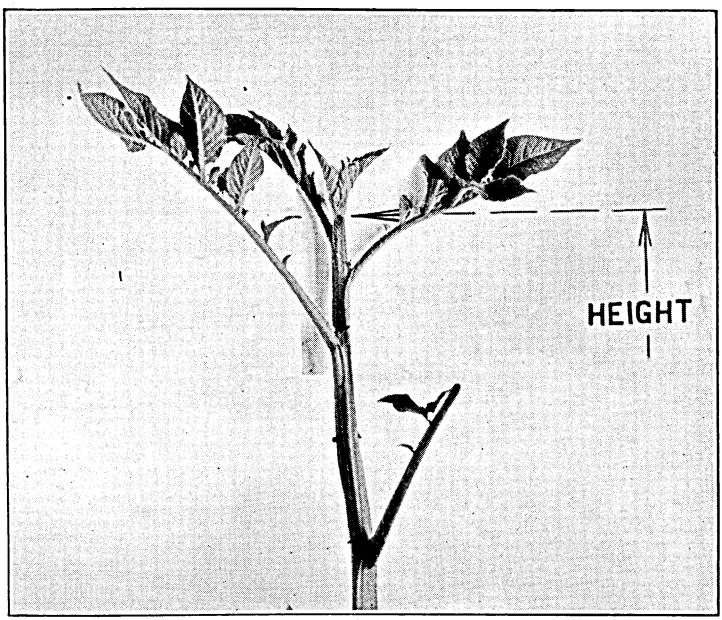

Fig. 4. Base of Terminal Cluster of Leaves, Which Offers a Relatively Definite Point from Which to Measure the Length of Stem

to overloads. The wicks on the humidity regulators gradually collected dust and had to be renewed every two weeks. Furthermore, it was necessary to add a small amount of mercuric bichloride to the distilled water supplied the wick to prevent growth of micro-organisms. These difficulties, combined with the fact that the chambers were

opened daily in measuring and watering the plants, resulted in actual conditions that were only approximations of the desired temperatures and humidities.

RESULTS

In both series of the main experiments the length of the stem was measured daily on ten plants. The stem was easily measured, as indicated in Figure 4, by taking the distance from the base of the terminal cluster of leaves to the top of the pot. To simplify measurements, branches were removed as soon as detected. These measurements are plotted in Figure 5.

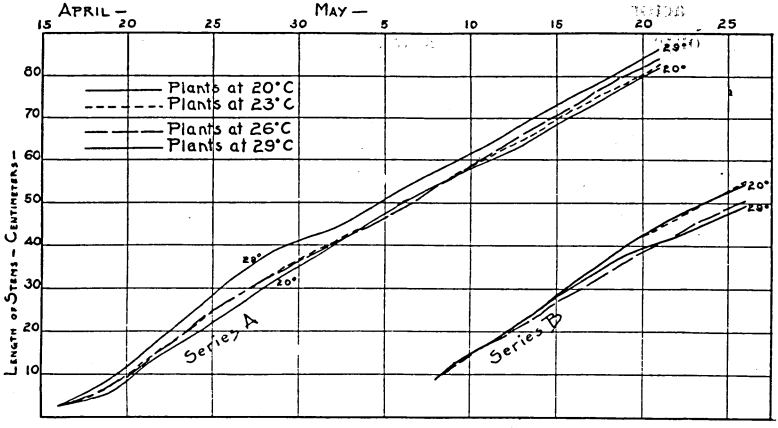

Fig. 5. Growth Curves of Stems

In series A the elongation of the stem during the first ten days of the measurements was more rapid at 29° than at the lower temperatures. This was most conspicuous during the first three days. In series B the plants were not moved to the chambers until they were about ten centimeters tall; thus the two series were not entirely comparable. The final measurements in the two were not in agreement, and as the differences in height were less than five centimeters, the results indicate that temperature had very little effect on the rate of elongation of the stem.

In addition to the plants in the chambers, a set of four plants was grown under the ordinary conditions of the cool greenhouse, parallel with series B except that the branches were not removed. They made a remarkably thrifty growth; evidently conditions were near the optimum for young potato plants. One of these is shown in Figure 6, with a typical plant from each of the temperature chambers. It can be seen in this figure that the height of the plants was not conspicuously affected by temperature. Similarly, under the range of conditions used here the number of nodes was approximately the same. Flower buds

appeared on all plants, abscissing without opening. The one striking effect of temperature was on size of leaflets. This is evident from Figure 6, but is more accurately shown in Figures 7 and 8. The leaflets were not only smaller at the higher temperatures but also lighter green. The differences are illustrated still more accurately by comparing the weight of leaflets with the total weight of the plants (Table III).

No explanation is offered at this point for the effect of high temperatures on the size of leaflets, but the reduction in photosynthetic area undoubtedly plays an important part in the reduced rate of tuber growth.

TABLE III

EFFECT OF TEMPERATURE ON WEIGHT OF LEAFLETS, AND RATIO OF WEIGHT OF LEAFLETS TO TOTAL WEIGHT OF ABOVE-GROUND PART OF THE PLANTS

	Temp. C.	Weight of plant, gm.	Weight of leaflets, gm.	Ratio, per cent
Series A.	May 27. Average of 3 plants from each temperature			
	20°	93	24	25.8
	23°	86	20	23.3
	26°	80	18	22.5
	29°	72	13	18.1
Series B.	May 15 to 20. Average of 7 plants from each temperature			
	20°	44.5	14.4	32.4
	23°	48.9	15.3	31.3
	26°	49.3	15.4	31.2
	29°	41.6	11.4	27.4
Series B.	May 21 to 27. Average of 9 plants from each temperature			
	20°	58.7	18.1	30.3
	23°	65.1	19.8	30.4
	26°	61.3	18.0	29.4
	29°	54.8	14.2	25.9

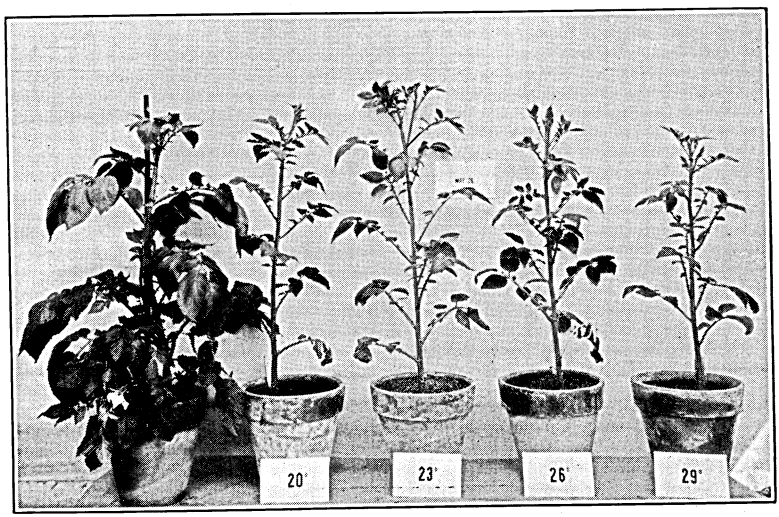

Fig. 6. Typical Plants from Series B

The plant with the large leaves was grown under ordinary cool greenhouse conditions, the others were from the chambers shown in Figure 3 at the temperatures indicated on the cards (Centigrade).

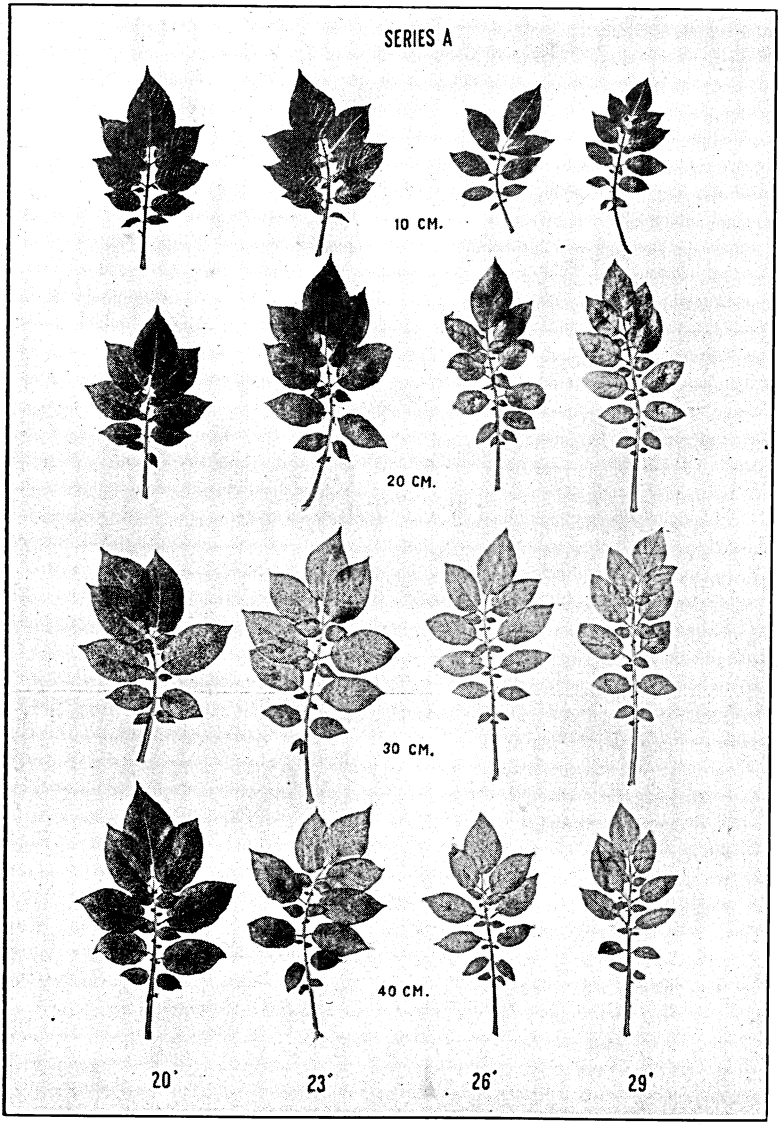

Fig. 7. Effect of Temperature on Size of Leaves at Different Points Along the Main Stem The measurements indicate the distance from the growing tip of the stem.

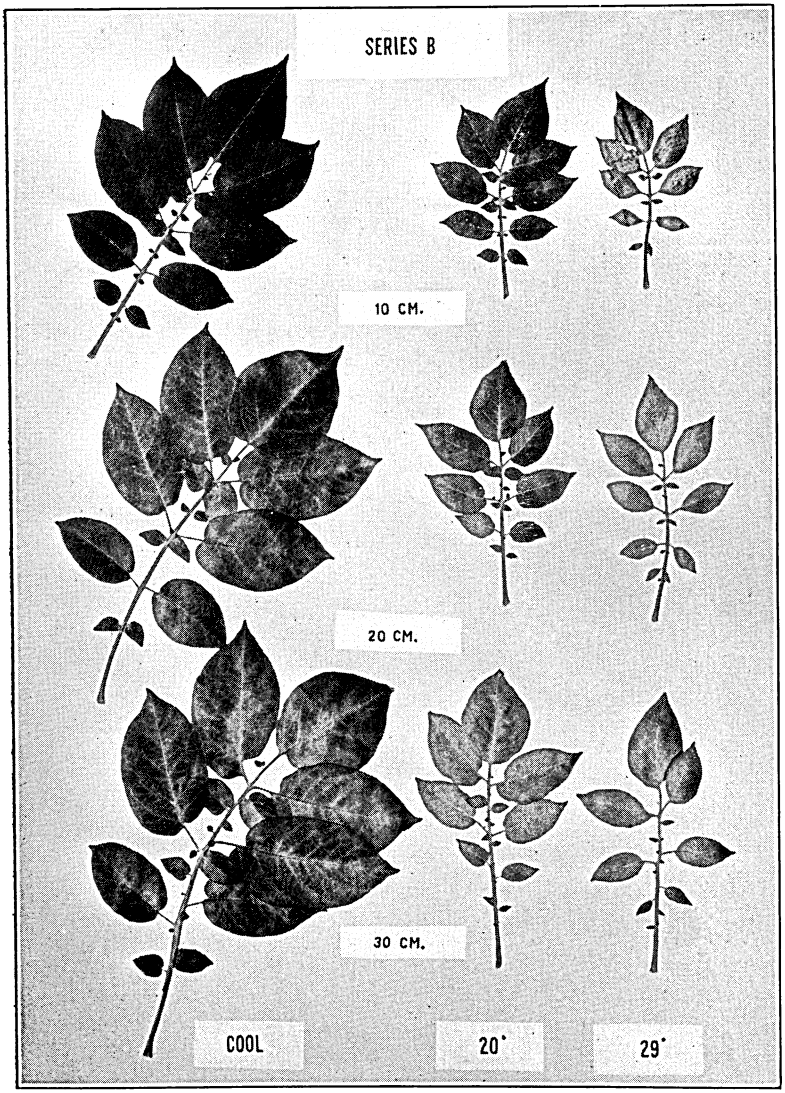

Fig. 8. Effect of Temperature on Leaves.

The large leaves were produced in a cool greenhouse, the smaller under incubator conditions at the temperatures given on the labels. Measurements are distances from the tip of the stem.

As pointed out earlier, it was necessary to discontinue the experiment with the advent of high temperatures, the last week in May. At this time the largest tubers on Series B were only about one centimeter in diameter. On Series A, however, the effect of temperature on the tubers showed clearly. (Fig. 9.) At 20° C. all of the plants had tubers two centimeters or more in diameter, while at 29° there was no swelling of the stolons. The average weight of these small tubers is given in Table IV.

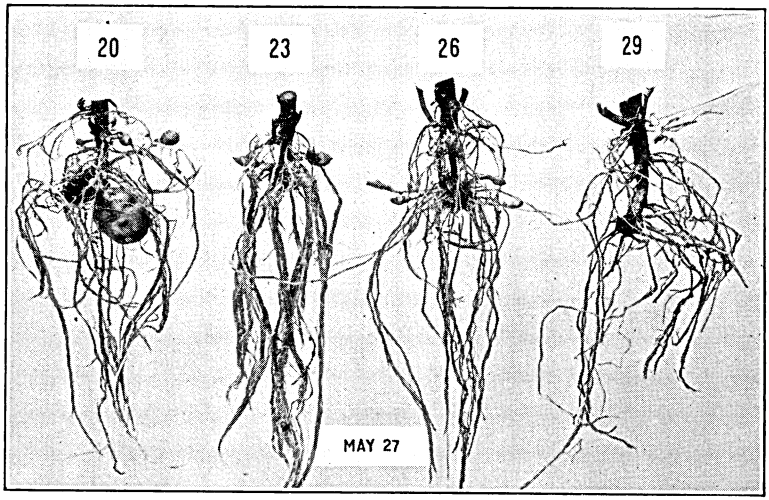

Fig. 9. Effect of Temperature on Early Stages of Tuber Growth

Photographed six weeks after the plants appeared above ground. Grown at the temperatures (C.) indicated by the figures.

TABLE IV

AVERAGE WEIGHT OF TUBERS PER PLANT. SERIES A. MAY 27

Temperature C.	Weight of tubers Grams
20°	20.9
23°	5.0
26°	1.6
29°	0.0

DISCUSSION

The evidence presented here agrees in all essentials with results reported in the literature. Temperature, by itself, is an important factor in tuber production by the potato plant. An interesting feature of these data is the reduction in size of leaflets at temperatures above the optimum. High temperature at any period after the plants are above ground reduces the size of the leaflets formed at that time, and this reduction in photosynthetic area undoubtedly has an effect on the yield of tubers.

However, the reduction in photosynthetic area was not sufficient to account for the depression in tuber growth at temperatures consistently above the optimum. Under the incubator conditions used here, the difference in tuber growth at any two temperatures was much greater than the difference in size of leaflets. Temperatures above the optimum were more detrimental to tuber development than to growth of other parts of the plant.

III. EFFECT OF TEMPERATURE ON RESPIRATION WITH REFERENCE TO TUBER GROWTH

No studies on the internal physiological reactions of the potato plant to temperature were reported in the literature reviewed in the introduction. Orton (18) suggested that high transpiration might explain the detrimental effect of summer heat, but this is not in accord with the evidence at hand showing that humidity is of relatively minor importance in yields. Since neither humidity nor rainfall has as much bearing on the rate of tuber growth as temperature, and since the effect of temperature is largely independent of moisture, its depressing effect is to be sought in something other than the water relations of the plant. As the tuber is largely *water plus starch,* attention has here been focussed on the production and storage of *starch.* This involves the photosynthesis, respiration, and translocation of carbohydrates by the plant as a whole.

LITERATURE

The literature on the relation of temperature to the physiological processes involved in production and storage of carbohydrates has been reviewed at length by Jost (11) and Kanitz (12) and briefly by Lehenbauer (14). The evidence from this literature leads to the conclusion that photosynthesis is not appreciably affected by the range of temperature under consideration here. The experiments of Matthaei (17), conducted under carefully controlled conditions, showed that in the cherry laurel leaf the rate of photosynthesis increased with increase in temperature over a considerable range when the atmospheric carbon dioxide was artificially increased. Under normal conditions, however, the low concentration of carbon dioxide was a limiting factor. This had been pointed out earlier by Brown and Escombe (4). Thus, with adequate light, increase in temperature accelerated the rate of photosynthesis up to the point where carbon dioxide became the limiting factor. In the case of the potato, however, the *decrease* in rate of starch storage begins at about 17° C. and becomes more and more pronounced the higher the temperature. There is nothing in the classical researches on photosynthesis to indicate that this decrease might be due to a lowering in the rate of carbohydrate synthesis.

On the other hand, the loss of carbon through respiration increases with rise in temperature. Respiration has been studied on various plant organs of a large number of species. In general, it is clearly a function of temperature. Matthaei's data from the work mentioned above are plotted in Figure 10. This curve illustrates the typical relation of temperature to respiration.

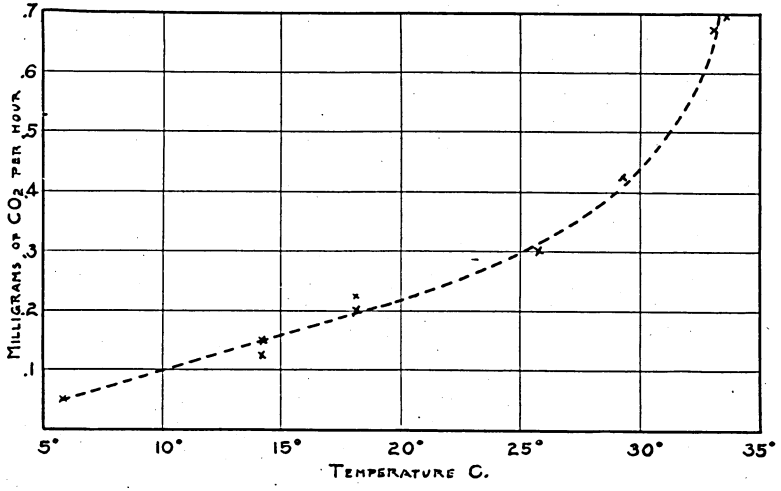

Fig. 10. Effect of Temperature on Rate of Respiration in Leaves of Cherry Laurel (Date of Matthaei 17)

The possibility that the respiration curve might account for the growth curve at temperatures above the optimum was pointed out by Blackman in 1905 (3). Calling attention to the various limiting factors at a growing region of the plant, he wrote:

"To take the hypothetical case that translocation could just bring in, per unit time, enough carbonaceous material for the growth at the optimum temperature *plus* the respiration at the same temperature. Then, as the temperature rose further and the respiration increased *faster and faster*, so necessarily there would be *less and less* carbon material available for growth. The falling curve of growth would become the complement of the rising curve of respiration, and it is of interest that to a large extent, whatever be its significance, the two curves actually have this appearance."

This hypothesis is substantiated by the fact that plants at high temperatures have a low carbohydrate content. Tottingham (23) has reviewed the literature on this point and presented data on buckwheat and clover grown under controlled conditions. Walster (26), also working with plants under controlled conditions, found a lower percentage of soluble carbohydrates and polysaccharides in barley at a temperature near 20° than near 15° C. The generalization is rather

well established: With increase in temperature above the optimum for growth there is a decrease in the soluble and readily hydrolyzable carbohydrates.

The evidence from several angles thus points to deficiency of carbohydrate as a limiting factor at temperatures above the optimum.

In the physiology of the potato plant the importance of this hypothesis is obvious, for the tubers are carbohydrate-storing organs. Any factor increasing the rate of respiration in any part of the plant would correspondingly decrease the carbon available for storage in the tubers. In the present work the problem has been attacked from this viewpoint, particular emphasis being laid on respiration.

ANALYTICAL METHODS

Respiration.—For respiration determinations the plants were disturbed as little as possible. The entire above-ground part of the plant was enclosed in a bell jar, the rim of which was embedded in a layer of paraffin covering the surface of the soil. In thus enclosing a plant it was necessary to remove it from the temperature chamber, apply melted paraffin containing a little rosin to the surface of the soil, cover with the bell jar, and replace it in its chamber. The temperature of the paraffin mixture was about 55° C. when applied, and apparently the stem was not injured by this treatment. The paraffin hardened in about 30 minutes. One plant from each temperature chamber was used for this determination each night from the time the plants were 25 centimeters tall until the close of the experiment, a period of about two weeks.

As soon as the paraffin mixture hardened, each bell jar was connected to a train of three absorption bottles containing strong solutions of sodium hydroxide, and carbon dioxide-free air was drawn through the system for thirty minutes. After this preliminary exhaustion of atmospheric carbon dioxide, an absorption tower, similar to that described by Truog (24), was connected into the system. With this apparatus it was a very simple matter to detect leaks. When the air inlet was closed at one end of the system, the bubbling in the absorption tower ceased if the set-up was air-tight. In a few cases leaks were found by this method, usually around the stem. The determinations on such individual plants were discontinued. As it required more than an hour to prepare a plant, no attempt was made to replace or repair these. In the absorption tower the carbon dioxide given off by the plant was absorbed in 50 milliliters of saturated solution of barium hydroxide. At the close of the determination the residual alkali was titrated with 0.1 normal hydrochloric acid containing one per cent barium chloride. At the close of the respiration period, the bell jar was

removed by melting the paraffin with hot water, and the plant was cut at the surface of the paraffin and weighed. The leaflets were then trimmed off and weighed separately.

Carbohydrates.—In sampling, ten grams of leaflets was rapidly clipped from each of three plants and this composite sample was preserved in hot alcohol containing a small amount of calcium carbonate. The leaflets were taken from the central portion of the plant, thus avoiding the older yellowed leaves and the young actively growing tissue. In a similar manner twenty grams of stems, including petiole, was taken from each plant.

The first steps of the analytical procedure followed the methods of Davis and Sawyer (7). The material was separated into two fractions by extraction with hot alcohol in a modified Soxhlet extractor. An aliquot of the extract was taken for dry matter determination. The balance of the extract containing the soluble sugars was then freed from alcohol by evaporation, taken up in water, clarified with neutral lead acetate, deleaded with disodium phosphate, and made up to volume. An aliquot was treated according to the A.O.A.C. method (1) with hydrodrochloric acid to hydrolyze sucrose.

The insoluble fraction from the extraction was dried, weighed, and part of it hydrolyzed with 1 per cent hydrochloric acid according to the suggestion of Spoehr and McGee (22). They found that in their material 1 per cent hydrochloric acid hydrolyzed the polysaccharide available to the plant for respiration. This method was not entirely satisfactory in potato samples, for the leaves exerted a buffer action that neutralized nearly half of the acid. With the stems this effect was negligible. However, samples from plants grown at different temperatures exerted nearly equal buffer action. The data are retained since there was considerable hydrolysis even at the reduced concentration of acid.

The determinations of reducing sugars were made according to the method of Shaffer and Hartmann (20). Their micro method was used because in some instances the samples were small and the sugar content was low. Klotz (13) reported that in his experience this method was not satisfactory. He stated that for analysis of a synthetic media for fungi the micro method gave "such variable results at different dilutions that it was entirely unsatisfactory for general use." The chief difficulty in the writer's experience arose from rapid titration. Unless the thiosulphate solution was added slowly and with rapid stirring, an excess of the thiosulphate would be added before the end point appeared. This occurred with pure glucose solutions as well as with plant extracts. It was found under the conditions of stirring employed that the thiosulphate solution should not be added at more than

10 milliliters per minute. Where the titration was carried on slowly, the error in the method, even at considerable dilutions, was less than 0.03 milligrams, as indicated in Table V.

TABLE V

EFFECT OF DILUTION ON SUGAR DETERMINATIONS OF POTATO LEAF EXTRACTS
Micro Method of Shaffer and Hartmann

	Sample A		Sample B	
	Found	Calculated	Found	Calculated
	mg.	mg.	mg.	mg.
Original concentration	1.53	....	1.43	....
One-half original concentration	0.74	0.765	0.72	0.715
One-quarter original concentration	0.36	0.383	0.35	0.358

RESULTS

Respiration determinations.—The data on rate of respiration are given in detail in Table VI. These determinations were restricted to series B. Series A was used for a number of preliminary tests but the data were too fragmentary to be included. The sunshine records in this table are from the Minneapolis office of the Weather Bureau, about five miles from University Farm. The green weight of leaves is given because of the great variation in size of plants. In selecting the plants for these determinations, those from the same position in their respective chambers were used rather than those of similar size. The variation in size is partly due to the fact that the ten most uniform plants were being reserved for measurements of growth response, leaving plants both larger and smaller than this modal group for the respiration experiments. From an inspection of the data, however, size of plant seems to have been a negligible factor in the rate of respiration.

TABLE VI

RATE OF RESPIRATION DURING THE NIGHT
Milligrams of CO_2 per 10 Grams of Leaves per Hour

Date	Hours of sunshine noon to sunset	Plants at 20°		Plants at 23°		Plants at 26°		Plants at 29°	
		Weight of leaves	CO_2	Weight of leaves	CO_2	Weight of leaves	CO_2	Weight of leaves	CO_2
May 13	0.4	11.0	3.55	11.0	4.66	11.5	*	8.0	4.85
14	2.5	11.0	3.50	11.5	4.85	11.5	*	8.0	5.98
15	1.5	12.5	3.33	16.0	3.65	17.0	4.05	12.5	3.08
17	5.8	12.5	5.34	19.0	6.27	17.0	6.13	9.0	6.06
18	1.3	18.5	3.71	16.0	5.17	11.5	*	11.5	*
19	0.8	18.5	3.14	16.0	3.58	11.5	*	11.5	4.42
20	6.4	11.5	5.19	10.0	6.17	11.5	6.59	11.0	7.01
21	2.9	5.5	6.07	12.0	6.13	10.0	6.30	5.5	6.88
22	6.0	8.5	4.74	17.0	6.35	16.0	6.41	18.5	6.47
24	4.8	17.0	5.82	18.0	5.92	22.0	6.36	11.5	6.83
25	5.7	21.0	5.12	17.5	5.56	18.0	6.70	15.5	8.71
26	6.4	23.0	6.53	24.0	7.33	15.5	7.52	16.0	9.25
Average: days of 4 hours or more sunshine after noon		...	5.46	...	6.27	...	6.62	...	7.39

* Leak.

When part of these data are summarized graphically as in Figure 11, the daily variations as well as the effect of temperature are illustrated more clearly. The daily variations appear to be in part associated with the age of the plants—the older the plants the higher the rate of respiration at all temperatures. Probably a more important factor is the difference in light intensity from day to day, for it may be noticed that the lower rates are in all instances from data obtained after cloudy days. The one exception was May 21, which is classed as a cloudy day with less than three hours of sunshine in the afternoon, but actually the sun shone brightly for about four hours near noon, and the respiration curve falls in the group following sunny days.

Anticipating that light intensity might play an important rôle, the respiration following the early cloudy days was analyzed in more detail by determining the carbon dioxide respired during the five hours before midnight and during a period of the same length after midnight. Later, comparable figures were secured following bright days. The data are summarized in Table VII.

TABLE VII

EFFECT OF LIGHT INTENSITY DURING THE AFTERNOON ON RATE OF RESPIRATION DURING THE NIGHT

Data are: (1) Milligrams of CO_2 per hour between 7 p.m. and midnight. (2) CO_2 per hour between midnight and 5 a.m. (3) Ratio of respiration before midnight to that after midnight, that is $\frac{(2)}{(1)}$

Temp. of plants:			20° C.			23° C.			26° C.			29° C.		
Date	Sunshine in p.m., hours		(1) 7-12	(2) 12-5	ratio	(1) 7-12	(2) 12-5	ratio	(1) 7-12	(2) 12-5	ratio	(1) 7-12	(2) 12-5	ratio
May 13	Cloudy	0.4	3.59	3.51	0.98	5.72	3.84	0.67	*	...	...	7.20	4.74	0.66
14	"	2.5	3.96	3.08	0.78	*	...	...	*	...	...	9.48	5.35	0.56
15	"	1.5	3.56	3.09	0.87	4.01	3.28	0.82	5.26	2.84	0.54	4.57	1.58	0.35
May 17	Sunny	5.8	5.74	4.89	0.85	6.45	5.91	0.92	6.08	6.18	1.02	6.56	5.45	0.83
20	"	6.4	5.91	4.47	0.76	6.49	5.84	0.90	6.71	6.46	0.96	5.01	9.01	1.80

* Leak.

After the cloudy days more carbon dioxide was respired in the five hours before midnight than in the five hours after midnight. Furthermore, the temperature effect was more conspicuous during the first five hours; the plants at the higher temperatures respired at a higher rate during the first five hours, and the greater the rate of respiration during this period, the greater was the decrease in rate after midnight. Following sunny days this change in rate did not occur; there was no significant drop in the rate of respiration after midnight. In one instance it increased at 29° C. This increase may have been due to a leak developing during the determination that escaped detection, or possibly the rate actually increased.

An obvious explanation of the change in rate of respiration following cloudy days is that the amount of respirable carbon compounds was

a limiting factor. On the basis of this hypothesis the respiration proceeded at a rate determined in part by temperature, and the higher the rate the sooner the supply of respirable material approached exhaustion and the sooner the rate declined. This did not occur after sunny days in spite of the higher initial rates of respiration, simply because of the greater supply of available photosynthate. The data are too meager to establish this hypothesis, but whatever the explanation may be, it is clear that the intensity of light during the day influenced the rate of respiration during the night.

In spite of the variations due to light and other causes, there is a general upward trend to most of the temperature-respiration curves of Figure 11. The one conspicuous exception, May 15, when the rate fell off at 29°, may have been due to low light intensity. The generalization is, then, conclusively established that within the range of temperature here studied, under incubator conditions, the higher the temperature the greater was the rate of respiration in the above-ground part of the plant.

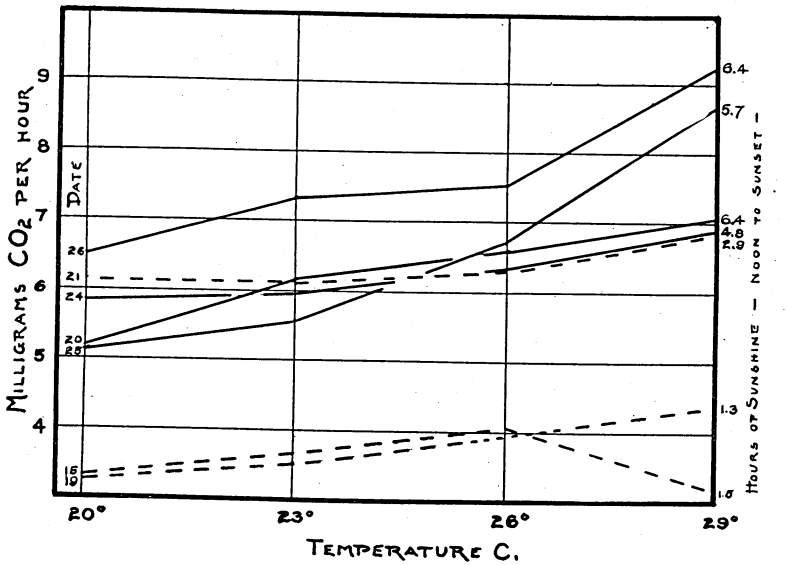

Fig. 11. Selected Data Showing Relation of Sunshine During Afternoon to Rate of Respiration the Following Night

Solid lines indicate sunny days; broken lines, cloudy days.

Carbohydrate determinations.—In these analyses the aim was to find the effect of temperature on the amount of respirable carbohydrate. The samples were therefore taken about sunset on days of bright light, May 20 and 26. The results are given in Table VIII. A conspicuous feature of these data is the consistently higher sugar content in the plants at 20° and 26° than at 23° and 29° C. Probably this was not

a temperature effect but due to differences in light, for in the arrangement of the chambers the 20° and 26°—those with the high carbohydrate content—were at the ends. (See Fig. 2.) They were purposely arranged in this order to check against variations arising from position that might have been interpreted as temperature effects if the chambers had been placed in a simple order of increasing temperature. As the data show a higher carbohydrate content in the end chambers, either these temperatures were more favorable to photosynthesis than 23° or 29°, or temperature effect was masked by some more important factor related to position—probably light.

TABLE VIII

CARBOHYDRATES AFTER SUNNY DAYS
CALCULATED ON A BASIS OF TEN GRAMS OF GREEN WEIGHT
Sugar values expressed as milligrams of glucose

Date	Temp. C.	Dry matter	Reducing sugar	Sucrose	Polysaccharides	Total
			Leaflets			
May 20, 8 p.m.	20°	1.011	7.5	12.2	15.3	35.0
	23°	0.947	6.7	6.8	11.3	24.8
	26°	0.960	12.1	10.7	13.7	36.5
	29°	0.830	7.9	7.4	9.9	25.2
May 26, 5 p.m.	20°	1.232	23.6	24.5	83.5	131.6
	23°	1.038	11.0	13.2	64.0	88.2
	26°	1.203	16.0	16.6	81.9	114.5
	29°	1.116	12.4	17.3	62.6	92.3
May 26, 6:30 p.m.	20°	1.139	7.7	22.6	78.4	108.7
	23°	1.065	7.0	13.7	66.2	86.9
	26°	1.117	20.3	14.4	70.0	104.7
	29°	1.106	13.0	13.7	58.6	85.3
			Stems and Petioles			
May 20, 8 p.m.	20°	0.495	21.0	7.6	24.0	52.6
	23°	0.432	14.4	6.2	23.2	43.8
	26°	0.478	20.0	7.4	25.2	52.6
	29°	0.403	12.6	5.4	20.1	38.1
May 26, 6:30 p.m.	20°	0.597	23.1	15.3	38.6	77.0
	23°	0.540	12.4	13.0	30.1	55.5
	26°	0.603	19.0	14.1	42.1	75.2
	29°	0.527	10.3	13.4	30.5	54.2

The evidence that light entered as a limiting factor, combined with similar evidence from the respiration data, suggests that light variations may in part account for the variations in the chemical determinations. The light was not uniform in all parts of the chambers because of shadows from the sash bars. Altho precautions were taken in both respiration and carbohydrate determinations to select plants from the same position in their respective chambers, there was undoubtedly considerable difference in the shading, and as a result differences were present that were not entirely temperature effects.

However, by assuming that the light in the two center chambers was the same, and comparing the carbohydrates in the plants at

23° with those at 29°, no conspicuous difference is evident in the carbohydrate content of either the leaves or stems. The polysaccharides hydrolyzed by one per cent hydrochloric acid are slightly lower at 29°, but the soluble sugars are slightly higher, and the totals therefore are not significantly different. Comparing the results from the two end chambers, operating at 20° and 26°, the conclusions are very similar; the differences are small. This interpretation leads to the general conclusion that the readily available carbohydrate content of the above-ground parts of these plants after a sunny day was not appreciably affected by this range of temperature.

TABLE IX

CARBOHYDRATES AT SUNRISE, MAY 27

Sugar values expressed in milligrams of glucose per ten grams of green weight

Temp. C.	Dry matter	Reducing sugar	Sucrose	Polysaccharides	Total
		Leaflets			
20°	1.175	8.2	1.1	40.0	49.3
23°	1.046	6.3	2.7	31.0	39.0
26°	1.174	4.5	12.2	41.0	57.7
29°	1.140	7.5	4.8	37.1	49.4
		Stems and Petioles			
20°	0.510	16.8	7.7	35.6	60.1
23°	0.448	4.5	3.1	29.9	37.5
26°	0.624	10.6	18.0	43.0	65.6
29°	0.486	6.3	5.3	30.8	42.4

To get a conception of the carbohydrates translocated during the night, the plants used for the respiration measurements of May 26 were sampled at the close of the determination, at sunrise May 27. They were sampled and analyzed in the same manner as the plants of the preceding evening, except that only one plant from each chamber was taken for the sample. A comparison of the analyses at sunrise, in Table IX, with those of the preceding evening, as presented in Table X, shows that about half of the carbohydrates of the leaves were lost during the night, and in the stems only a small reduction in carbohydrates took place. Here, again, the temperature effect is not conspicuous. The differences, representing the carbohydrate translocated and respired during the night, are somewhat greater at the lower temperatures, but are complicated by the variations present in the evening. Altho the data are meager, they indicate that utilization of carbohydrates during the night in translocation plus respiration proceeds somewhat more rapidly at the lower temperatures. But the differences are small and not so outstanding as the fact that a considerable quantity of readily available carbohydrate was present in the leaves and stems at sunrise at all of these temperatures.

TABLE X

COMPARISON OF CARBOHYDRATES AT SUNSET AND SUNRISE
From Data of Tables VIII and IX

Temp. C.	Total carbohydrate 6:30 p.m.	5:00 a.m.	Difference
	Leaflets		
20°	108.7	49.3	59.4
23°	86.9	39.0	47.9
26°	104.7	57.7	47.0
29°	85.3	49.4	35.9
	Stems and Petioles		
20°	77.0	60.1	16.9
23°	55.5	37.5	18.0
26°	75.2	65.6	9.6
29°	54.2	42.4	11.8

The slow translocation can not be attributed to the artificial environment. Davis and Sawyer (7) reported similar data from plants growing in the field. Their analyses were of plants at an early stage of development, probably comparable to those used here, but at an average temperature nearer the optimum for tuber growth, about 15° C. Furthermore, they used larger samples and separated the different carbohydrates in greater detail. When summarized, as in Table XI, their data show a very small difference between the sum of the carbohydrates at sunset and sunrise. Altho their data on a dry weight basis are not readily comparable with the figures above from a green weight basis, and neither gives the absolute amounts, the results do show that the leaves and stems contain a relatively high percentage of soluble and hydrolyzable carbohydrate at sunrise, indicating that a correspondingly small percentage has been translocated and respired during the night.

TABLE XI

CARBOHYDRATES AT SUNSET AND SUNRISE, DATA OF DAVIS AND SAWYER (7)
Values expressed in percentage of dry matter

	Leaflets		Stems	
	At 8 p.m.	At 4 a.m.	At 8 p.m.	At 4 a.m.*
Hexoses	1.22	0.15	5.63	4.30
Sucrose	2.73	1.76	3.57	2.34
Pentose	0.42	0.43	0.53	0.82
Pentosan	5.51	5.70	12.15	12.08
Starch	1.61	1.33	0.13	0.78
Soluble starch	0.36	0.00	...	...
Total	11.85	9.37	22.01	20.32
Loss during night		2.48		1.69
Expressed in per cent		20.9		7.7

* Davis and Sawyer made no analyses of stems sampled at 4 a.m. These figures are calculated by extrapolation from analyses of 2 a.m.

Relation of respirable carbohydrate to respiration.—The carbohydrates reported in the preceding analyses can not be quantitatively compared with the respiration, for the carbohydrate samples included only a portion of the leaves and stems while the respiration figures are based on the entire above-ground parts. However, comparative calculations are interesting and show more clearly the importance of respiration to carbohydrate storage. For a standard of comparison, the data in Table XII have been calculated on a basis of ten grams of green weight of leaflets and the carbon dioxide of respiration (from Table VI) is reduced to its glucose equivalent. To secure a representative fraction of the entire top based on ten grams of leaflets, it was necessary to include somewhat more than twenty grams of stems. The actual weight of stem corresponding to ten grams of leaflets for each sample is shown in the table. Here the decrease in carbohydrate in the leaflets during the night is added to the decrease in the stems, and the totals are compared to the respiration.

TABLE XII

RELATION OF RESPIRATION TO CARBOHYDRATE LOST FROM LEAVES AND STEMS DURING THE NIGHT OF MAY 26-27

All values calculated to a basis of ten grams of green leaflets

Temperature	20° C.	23° C.	26° C.	29° C.
Leaflets				
Total carbohydrate at 6:30 p.m., mgm.	108.7	86.9	104.7	85.3
5:00 a.m.	49.3	39.0	57.7	49.4
Decrease	59.4	47.9	47.0	35.9
Stems and Petioles				
Weight per 10 gm. leaflets at 6:30 p.m. gm.	21.7	22.0	24.5	28.2
5:00 a.m.	23.8	24.6	25.6	28.7
Total carbohydrate at 6:30 p.m. mgm.	167.0	122.1	184.0	152.8
5:00 a.m.	143.1	92.3	167.9	121.5
Decrease	23.9	29.8	16.1	31.3
Total decrease—carbohydrate lost from the above-ground parts during the night	83.3	77.7	63.1	67.2
Respiration. Glucose equivalent	44.6	50.0	51.2	63.1
Percentage of total decrease	53.5	64.4	81.0	93.9

The respiration during the night, as indicated by these calculations, accounts for 53 to 94 per cent, according to temperature, of the decrease in the carbohydrates from sunset to sunrise. The temperature effect is conspicuous. The balance left for growth and storage is about 46 per cent at 20° and only 6 per cent at 29° C. In other words, the carbohydrate available for growth and storage during this night was more than seven times greater at 20° C. than at 29° C.

Even tho these calculations are only approximations, they are strong evidence supporting the view that the detrimental effect of high temperature on tuber growth in the potato is in a large measure due to losses of carbon through respiration.

DISCUSSION

The general inter-relationship between temperature, photosynthesis, respiration, and translocation, found in these studies, is graphically summarized in Figure 12. The two curves of this graph are smoothed averages of data illustrating the physiological situation during the night. The straight line represents the difference between the carbohydrate found in leaves and stems at sunset and at sunrise—the carbohydrate lost from the tops during the night. The ascending curve represents the carbohydrate equivalent of the respiration during the same period. The carbohydrates translocated for growth and storage at a given temperature are then represented by the distance between the two curves at that temperature.

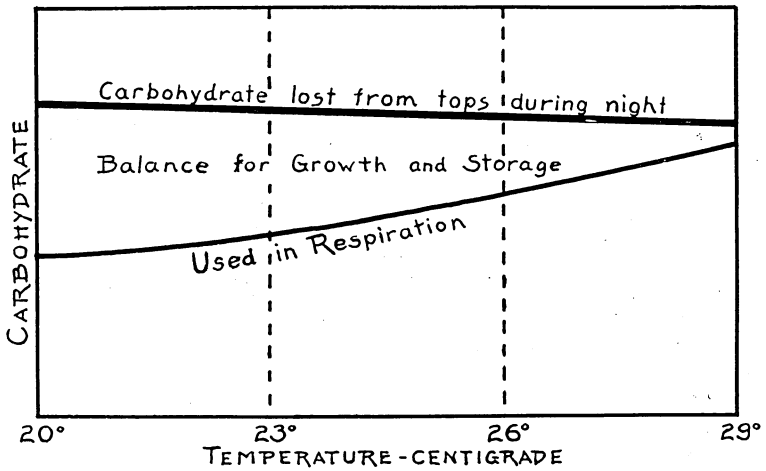

Fig. 12. Relation of Respiration to Total Photosynthate Moved from the Leaves and Stems During the Night

The importance of this inter-relation lies in the fact that the curve of carbohydrate available for growth and storage, as shown by this graph, roughly fits the curve of tuber growth. This fit suggests that tuber growth is directly related to the available carbohydrate.

The data from which these curves were drawn treat only of the situation during the night. No analyses were made during the day except those at sunrise and sunset. In these there was no significant temperature effect; the accumulation of carbohydrate in the leaves and stems during the day was approximately the same at 20° as at 29° C. This fact may be taken to indicate that photosynthesis was also unaffected by temperature. As studies on photosynthesis in other species have shown that deficiency of carbon dioxide or deficiency of light may be limiting factors, it is entirely probable that photosynthesis was limited here, and consequently the total carbohydrate produced during

the day may have been approximately the same throughout this range of temperature. If photosynthesis was thus limited, and if respiration increased with temperature, as it did at night, then the general relation illustrated in Figure 12 may apply to the period of daylight as well as the period of darkness.

This view re-emphasizes the importance of the carbohydrates in relation to the rate of tuber growth. The deficiency of carbohydrate was very probably the limiting factor at these temperatures.

In a generalized form this hypothesis may have wide application in plant physiology. Considerable literature supports the view that deficiency of carbohydrate may be a limiting factor in growth of plants at temperatures above the optimum. The evidence is not direct and conclusive, but falls into three significant lines: (1) Respiration increases with temperature. (2) Photosynthesis is not continuously a function of temperature, deficiency of available carbon dioxide entering at some point as a limiting factor. (3) At high temperatures the carbohydrate content of plants is relatively low. These three facts point to the generalization that deficiency of carbohydrate is a limiting factor in growth of plants at high temperatures.

In studies carried on under artificial conditions the question arises: How far are the conclusions applicable to field conditions? In the case of the potato, the growth under ordinary greenhouse culture appears to be in every way normal. But under the incubator conditions used here, the plants were more spindling than normal, indicating a deficiency of light. It is very probable that the two layers of glass and the shade of the sash bars reduced the light below the optimum for photosynthesis. It is also possible that respiration was abnormally high, as suggested by Brown and Escombe (5). Either of these conditions would reduce the carbohydrate available for growth and storage, and thus reduce tuber growth. In the field there is probably more growth at these temperatures than occurred in the chambers. Thus, in the field, some tuber growth may occur at 29° C., altho none occurred in the chambers at this temperature. A further point to be considered is that this experiment dealt only with young plants. It is possible that older plants would not be so sensitive to temperature. But even taking into consideration these possibilities, the evidence still points to deficiency of carbohydrate as a limiting factor in tuber production at temperatures above the optimum, in the field as well as in the greenhouse.

IV. SUMMARY

1. Evidence in the literature dealing with the relation of temperature to potato yields indicates: (a) The optimum temperature for tuber yield is near 17° C. (b) Above 17° C. yields rapidly decrease with increase in temperature. (c) The detrimental effect of high temperature is largely independent of moisture.

2. In the experiment reported here, potato plants were grown in thermoregulated chambers set to operate at 20°, 23°, 26°, and 29° C.—a range of temperature above the optimum.

3. The plants showed conspicuous responses in the leaves and in the tubers, both decreasing in size with increase in temperature. At 29° no tubers formed. The maximum temperature for tuber growth under these conditions was thus between 26° and 29° C.

4. Respiration during the night in the above-ground part of the plant increased with temperature.

5. The carbohydrate content of leaves and stems, sampled at both sunset and sunrise, was not appreciably affected by this range of temperature.

6. The reduction in the carbohydrate available for translocation which resulted from the increased respiration at the higher temperatures, roughly corresponded to the reduction in tuber growth. Thus, the rate of tuber growth appeared to be a function of the available carbohydrate.

7. From these data, together with evidence from the literature, the suggestion is made that deficiency of carbohydrate arising from excessive respiration may be very generally the limiting factor in plant growth at temperatures above the optimum.

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STAFF OF DIVISION OF HORTICULTURE

W. H. ALDERMAN, B.S.A., Horticulturist

Section of Vegetable Gardening

F. A. KRANTZ, Ph.D., Assistant Horticulturist
*JOHN BUSHNELL, Ph.D., Assistant Horticulturist
BASIL I. BURRELL, B.S., Assistant Horticulturist
H. J. TRAUB, M.S., Assistant Horticulturist

Section of Pomology

W. G. BRIERLEY, M.S., Associate Horticulturist
A. C. HILDRETH, B.S., Assistant Horticulturist

Section of Fruit Breeding

J. H. BEAUMONT, Ph.D., Assistant Horticulturist
A. N. WILCOX, M.S., Assistant Horticulturist

Section of Floriculture and Landscape Gardening

CLARENCE E. CARY, B.S. in Agr., Assistant Horticulturist
L. SANDO, Florist
F. E. HARALSON, Assistant Superintendent, State Fruit Breeding Farm

* Resigned.